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**Title: Some mistakes go unpunished: the evolution of “all or nothing”  
signalling**

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**Running title:** evolution of “all or nothing” signalling

**Abstract**

Many models of honest signalling, based on Zahavi’s handicap principle, predict that if receivers are interested in a quality that shows continuous variation across the population of signallers, then the distribution of signal intensities will also be continuous. However, it has previously been noted that this prediction does not agree with empirical observation in many signalling systems, where signals are limited to a small number of levels despite continuous variation in the trait being signalled. Typically, there is a critical value of the trait, with all individuals with trait values on one side of the threshold using the same cheap signal, and all those with trait values on the other side of the threshold using the same expensive signal. It has already been demonstrated that these classical models naturally predict such “all-or-nothing signalling” if it is additionally assumed that receivers suffer from perceptual error in evaluating signal strength. We show that such all-or-nothing signalling is also predicted if receivers are limited to responding to the signals in one of two ways. We suggest that many ecological situations (such as the decision to attack the signaller or not, or mate with the signaller or not) involve such binary choices.

**Keywords:** signaling, signal honesty, Zahavi’s handicap principle, communication, cost of signalling

## 46    **Introduction**

47    Game theoretical models based on Zahavi's handicap principle have been very  
48    influential in offering an explanation for how signalling can remain (on average)  
49    honest when there is conflict of interest between signaller and receiver (Maynard  
50    Smith & Harper 2003; Searcy & Nowicki 2005) . Johnstone (1994) raised an  
51    interesting comparison between the predictions of still-influential models and  
52    empirical observation. Models generally predict that the intensity of the signal will  
53    vary continuously in relation to the quantity being signalled. For example, in a  
54    situation where potential prey individuals vary continuously in the strength of their  
55    chemical defences, these models would predict a similar continuous distribution of  
56    warning signal intensities to potential predators. To express this another way, these  
57    models predict that the signals should provide exact quantitative information about the  
58    specific defensive capability of each signaller. In contrast, Johnstone (1994) provides  
59    numerous empirical examples of signals where observed variation in signal strength is  
60    much less: being confined to a small number (often two) of discrete signal strengths.  
61    In the context of our example above, this would suggest that even if there is strong  
62    and continuously-distributed between-individual variation in the strength of the  
63    defences being signalled, the potential prey only adopt one of two signal intensities.  
64    All those individuals with defence levels below some threshold value produce  
65    essentially identical signals of the same low intensity; all those with defence values  
66    above the threshold signal at the same characteristic high intensity. In comparison to  
67    the model predictions then, real signals often seem less quantitatively informative.  
68    They inform the receiver not about the specific quality of an individual signaller but  
69    only about the range of qualities (either above or below the threshold in the example  
70    above) in which the individual falls.

Johnstone (1994) not only drew attention to this apparent tension between model predictions and empirical observations, he also offered a plausible solution. He demonstrated that previous models had assumed that the receiver identifies the intensity of the signal with perfect fidelity. If, however, perceptual errors are introduced into these models, such that the receiver can make errors in their evaluation of the signal intensity, then the predictions of the models change to being much more in line with the “all or nothing” displays often seen in nature. Such perceptual errors are very plausible (Dusenbury 1992; Hailman 2008).

Here we make no criticism of Johnstone’s (or any other previous) work but present another modification to previous models which we argue is biologically realistic, very widely applicable and again leads to a prediction of “all or nothing” displays even when no perceptual errors are assumed in the model. Essentially our key modification rests in the evaluation of optimal predator behaviour. Like previous works, Johnstone assumed that the optimal strategy for the receiver was that which minimized the least-square estimate of signaller quality for each perceived advertising level. That is, the receiver is expected to be selected to evaluate the underlying quality of all individuals as accurately as possible, and all deviations from accurate estimation are in some way costly to the receiver. We suggest that there are many biological situations where the challenge facing the receiver is less strict and some mis-evaluations produce no fitness cost.

Consider again the predator that encounters individuals from a prey population that vary continuously in their level of chemical defence. On encountering a potential prey individual, the predator must make a binary decision: to eat the individual or not. If the predator somehow had complete and perfect knowledge of the level of chemical defence in each prey individual then the most rational strategy is to identify the

96 minimum level of defence that makes a prey individual unattractive, then eat all  
97 individuals with levels below this threshold and reject all those with levels above it  
98 (Skelhorn & Rowe 2007). The problem for most real predators is that they do not  
99 have this perfect knowledge, rather they must make their decisions based on each  
100 individual's level of signalling (Mappes et al 2005). Let us imagine that the level of  
101 defence can vary between zero and one and the threshold value discussed above is  
102 denoted by  $T$ . The challenge facing the predator is not to evaluate the defence level of  
103 each encountered individual as accurately as possible, but rather to make as few  
104 misclassifications as possible as it attempts to classify each individual as having a  
105 defence level either above or below  $T$ . Another way to look at this is that (unlike the  
106 formulation of Johnstone 1994 and other models) not all mistakes in the estimation of  
107 a prey individual's level of defense incur fitness costs for the predator. If the true level  
108 of defence is  $D$  and the predator estimates the defence as a different value  $d$ , then this  
109 error only has fitness consequences for the predator (it only changes its behaviour) if  
110  $D$  and  $d$  bracket the threshold value  $T$ , otherwise the inaccuracy of estimation has no  
111 effect. Further, it may be that the cost of a misclassification to the predator depends  
112 upon the value of  $D$ , but the value of  $d$  has no effect on the size of this cost, except in  
113 influencing whether or not misclassification occurs (and thus whether or not the cost  
114 is paid). Thus, we suggest that models where receivers can only produce a discrete  
115 number of responses to the signal might reasonably involve the assumption that  
116 fitness is affected not by accurate estimation of the qualitative value of the underlying  
117 quality of signallers, but by the less onerous task of correctly classifying prey into a  
118 number of distinct categories. We expect that this situation will occur commonly,  
119 where a receiver must make a simple binary choice (e.g. to attack or not, to mate or

not, to abandon a nest or not). Here we will explore the consequences of this change of fitness function for model predictions.

## **Model description**

For ease of comparison we have attempted to keep our model definition and structure as close to that of Johnstone (1994) as possible.

We suppose that signallers vary in some quantity that is of interest to receivers, but which they cannot directly observe. We denote the value of this quantity held by a specific individual as  $q$  (for quality). Signallers can vary in the intensity of some signal that can be directly observed by receivers, with the signal given by a specific individual being denoted  $a$  (for advertising). We denote the function  $A(q)$  as the signalling strategy, which specifies the signal intensity (the value of  $a$ ) given by individuals of different qualities (different values of  $q$ ).

On receipt of the signal from a specific signaller, the receiver can act in one of only two distinct ways (we denote these alternatives “choice 0” and “choice 1”). The receiver strategy is described by  $g(a)$ , which is the probability of making choice 1 on receipt of a signal of intensity  $a$ . By definition, an individual which does not make choice 1 must make choice 0, and vice versa. Unlike Johnstone (1994), we assume perfect fidelity of signal transmission, so if the signaller sends a value  $a$ , the receiver receives exactly that same value.

144 The reward  $U$  that a signaller gets from an interaction with the receiver depends on its  
 145 quality  $q$ , the signal strength it used  $a$ , and the response of the receiver (either 0 or 1).  
 146 Thus the reward to the signaller is  $U(a,i,q)$ , where  $i$  is the response of the receiver:  $i$   
 147  $\in \{0,1\}$ .

148

149 We assume that choice 1 by the receiver is always more beneficial to the signaller  
 150 than choice 0. That is  $U(a,0,q) < U(a,1,q)$  for all combinations of  $a$  and  $q$  values. Thus  
 151 in our previous example, choice 1 is rejection of the signalling prey by the predator.  
 152 We also assume that the advantage of choice 1 over choice 0 to the receiver does not  
 153 decrease with  $q$ , i.e.

154

$$155 \quad \frac{\partial(U(a,1,q) - U(a,0,q))}{\partial q} \geq 0. \quad (1)$$

156 For example, a high-quality male will have at least as large a gain from mating over  
 157 not mating as a lower-quality male. This seems generally likely to be true for mating  
 158 systems. For our predator-prey example, the difference between choice 1 and choice 0  
 159 is between persuading the predator not to attack versus being attacked. In this case,  
 160 condition (1) means that even very highly defended prey benefit from persuading the  
 161 predator not to attack at least as much as weakly defended prey do. Whilst it may be  
 162 that very highly defended prey can survive attacks because the predator discovers the  
 163 level of defence during the attack and thus aborts the attack, even such abortive  
 164 attacks can be costly to prey in terms of risk of injury and/or time and energy wasted.  
 165 Further, in some situations the predator may have already killed the prey before  
 166 aborting the attack when realizing that the particular prey item is too defended to be  
 167 eaten. Thus condition (1) seems plausible in a predator-prey context too.



168

169 We further assume that signals are expensive to the signaller, and that this expense  
 170 increases (and so the net reward from an interaction decreases) with increasing  
 171 signalling intensity. Thus we assume that for all combinations of (a,i,q),

172

$$173 \quad \frac{\partial U(a, i, q)}{\partial a} < 0. \quad (2)$$

174 We also assume that the cost of higher signal intensity is proportionately greater for a  
 175 lower quality individual:

176

$$177 \quad \frac{\partial^2 U(a, i, q)}{\partial q \partial a} > 0. \quad (3)$$

178 These assumptions about the costs of signalling are those generally considered as  
 179 requirements for honest signalling via the handicap model (Grafen 1990, Bradbury &  
 180 Vehrencamp 1998, Searcy & Nowak 2005; but see Lachman et al 2001 for an  
 181 exception).

182

183 The reward to a signaller of quality q that signals with intensity a is given by

184

$$185 \quad S_q(a) = g(U(a, 1, q)) - g(U(a, 0, q)) \quad (4)$$

186

187 We assume that there is only a single type of receiver in our model, so that for  
 188 instance receivers do not vary in quality and hence in their reward functions. We also  
 189 assume the reward to the receiver from an encounter is a function of the quality of the

signaller  $q$  and the receiver's decision  $i$ , which we shall denote by  $V(q,i)$ , and that the higher the quality of the signaller (the higher  $q$  is) the better it is for the receiver to make choice 1. That is  $V(q,1) - V(q,0)$  increases with  $q$ . In our example, the more defended the prey individual the more advantageous it is for the predator to reject the opportunity to eat it.

Let  $f(q)$  describe the frequency distribution of signallers of different qualities in the local population (which the receiver encounters randomly). The expected receiver reward is a function of its strategy ( $g$ ) and is given by

$$R(g) = \int f(q) [V(q,0) - g(A(q))] dq + \int f(q) [V(q,1) - g(A(q))] dq \quad (5)$$

$$= \int f(q) [V(q,0)] dq + \int f(q) [V(q,1) - V(q,0)] g(A(q)) dq$$

where integrals are evaluated over all possible values of signaller quality. We shall assume that in the absence of any signal the receiver will always make choice 0 (e.g. predators must always attack some prey to survive, so in the absence of a signal they will attack all prey rather than none), i.e.

$$\int f(q) [V(q,0)] dq > \int f(q) [V(q,1)] dq \quad (6)$$

### Model evaluation

We know that  $V(q,1) - V(q,0)$  increases with  $q$ ; let us suppose in particular that  $V(q,1) - V(q,0) < 0$  if and only if the quality of the signaller is below some critical value  $q_{crit}$ , so we have

$$V(q_{crit}, 0) \geq V(q_{crit}, 1). \quad (7)$$

215

216 Thus the receiver would benefit from making choice 0 if and only if  $q < q_{crit}$ .

217

218 Any strategy of the receiver must specify how it responds to every possible signal.

219 Denote the set of all signals  $a$  for which the receiver actually makes choice 1 as  $A_1$ ,

220 and the set of all signals for which the receiver makes choice 0 as  $A_0$ .  $A_1$  and  $A_0$  are

221 disjoint sets (no possible signal appears in both sets), and all possible signals are a

222 member of either  $A_0$  or  $A_1$ .

223

224 Since receivers respond to all signals in  $A_1$  identically, but signals are increasingly

225 costly (inequality (2)) to senders as signal intensity increases, the only rational signal

226 in the set  $A_1$  for a signaller to give is the lowest intensity (cheapest) signal in that set:

227 which we denote  $\min(A_1)$ . Similarly since receivers respond to all signals in  $A_0$

228 identically, but signals are increasingly costly to senders as signal intensity increases,

229 the only rational signal in the set  $A_0$  for a signaller to give is the lowest intensity

230 (cheapest) signal in that set: which we denote  $\min(A_0)$ .

231

232 Since  $U(a, 0, q) < U(a, 1, q)$  for all combinations of  $a$  and  $q$  values, for  $\min(A_0)$  to be

233 optimal for any  $q$ , this implies that  $\min(A_0) < \min(A_1)$ ; that is that the signal associated

234 with the less favourable receiver choice 0 must be of lower cost, and so at a lower

235 intensity, than that associated with the more favourable choice 1. Since all possible

236 signals are in either  $A_0$  or  $A_1$ , the signal associated with 0 will be the cheapest signal

237 of all the possible signals that are open to those individuals ( $A_1 \cup A_0$ ). Thus if the

238 lowest cost signal is  $a = 0$ , then  $\min(A_0) = 0$ . Let us further define  $a_1 \equiv \min(A_1)$ .

Clearly  $a_1$  must be greater than zero. Thus there are at most two distinct signals in any evolutionarily stable signalling system. A necessary qualification at this point is that this is only true when receivers do not vary in quality to a sufficient degree that different receivers would ideally like to respond to many different signallers in different ways. If there is wide receiver variation, our results would no longer be valid. For instance Johnstone & Grafen (1992) consider the Sir Philip Sidney game where the choice to receivers is to donate food to a relative or not. All receivers survive if they do not donate (and all signallers survive if they receive a donation), but some receivers (signallers) are almost guaranteed to survive if they donate (do not receive), and others are almost guaranteed to die. Under such circumstances, assuming high relatedness, different receivers would “want” to make different decisions to a wide range of signallers (equivalent to having very different values of  $q_{crit}$  in our model), and consequently their model has a continuous signalling solution.

It should be noted that our argument about the number of distinct signals generalizes to a system where the receiver has any finite number of decisions  $n$ . If we denoted the set of all signals for which the receiver would respond with choice  $i$  by  $A_i$ , then the only potentially consistent signal choices by the signallers would be  $\min(A_i)$ , and so the maximum number of distinct signals would be  $n$ .

Now let us suppose that we have an “honest” signal, namely one that distinguishes the signallers for which the receiver would want to make choice 0, from those for which choice 1 would be best. This would yield

$$g(A|q) = \begin{cases} 1, & q > q_{\text{crit}} \quad A \in A_1 \\ 0, & q < q_{\text{crit}} \quad A \in A_0 \end{cases} \quad (8)$$

264

265 When the receiver plays this strategy then the reward to the signaller simplifies to

266

$$S_q(A) = \begin{cases} U(A, 0, q) & a \in A_0 \quad q < q_{\text{crit}} \\ U(A, 1, q) & a \in A_1 \quad q > q_{\text{crit}} \end{cases} \quad (9)$$

268

269 Thus the optimal signalling strategy associated with an honest signal should be

270

$$A(q) = \begin{cases} \min(A_0) = 0, & q < q_{\text{crit}} \\ \min(A_1) = a_1 > 0, & q > q_{\text{crit}} \end{cases} \quad (10)$$

272

273 For there to be a stable signalling strategy where all  $q < q_{\text{crit}}$  individuals pick 0 and all

274  $q > q_{\text{crit}}$  individuals pick  $a_1$ , for some positive  $a_1$ , we need both choices to offer the

275 same reward to the signaller when  $q = q_{\text{crit}}$  (otherwise individuals of quality either just

276 above or below  $q_{\text{crit}}$  could do better by switching signal). Thus we need

277

$$U(a_1, 1, q_{\text{crit}}) = U(0, 0, q_{\text{crit}}). \quad (11)$$

279

280 Since  $U(a_1, 1, q)$  decreases with increasing  $a_1$ , there is at most one value of  $a_1$  that

281 satisfies (11). Such a value will exist provided there is such a critical quality value  $q_{\text{crit}}$

282 where the receiver would want to change their strategy, and that the largest signals are

283 sufficiently costly, so that  $U(\infty, 1, q_{\text{crit}}) < U(0, 0, q_{\text{crit}})$ . Thus  $[0, a_1) \subseteq A_0$  and  $a_1 \in A_1$ . In

284 fact we shall assume the natural solution of  $A_0 = [0, a_1)$  and  $A_1 = [a_1, \infty)$ .

285

286 Inequalities (1) and (2) ensure that for lower quality individuals the relative costs of  
287 signalling compared to the benefits of receiving choice 1 are higher, and consequently  
288 any individual of quality  $q < q_{\text{crit}}$  would do worse by changing its signal to  $a_1$  or any  
289 other value in  $A_1$ , and any individual of quality  $q > q_{\text{crit}}$  would also do worse by  
290 switching signal. Note that the combination of (1) and (2) are sufficient but not  
291 necessary, so that the relative costs compared to benefits may decrease with quality  
292 even if only one of the two conditions hold.

293

294 Note that the exact composition of the sets  $A_0$  and  $A_1$  in such a system depends upon  
295 how rogue signals not equal to 0 or  $a_1$  come about. Any individual that uses such a  
296 signal is behaving sub-optimally, so we would expect such situations to be rare. The  
297 exact solution in these rare cases would depend upon assumptions about the  
298 underlying causes of such irrational behaviour (see Discussion).

299

300 It should also be noted that only two signals are used at equilibrium, and that if there  
301 are no rogue signals as described above, every receiver strategy that responds to these  
302 two signals in the same way thus performs equally well at the equilibrium, regardless  
303 of how they respond to other signals. We assume that there will be a low level of such  
304 “mistakes” which means that all receivers have to play optimally against the “non-  
305 played” strategies themselves. This idea is often used in game theoretical modelling,  
306 and is known as the “trembling hand” (Selten, 1975).

307

308 It is possible to envisage a signalling system that is not entirely honest. For stability  
309 all low-quality individuals must play 0, and all high quality individuals must play

310  $\min(A_1)$ ; but perhaps there can be a cut-off point  $q^*$  that is different to  $q_{\text{crit}}$ . If we  
 311 replace  $q_{\text{crit}}$  by  $q^*$  in (8-11), we would obtain a different equilibrium signalling system  
 312 with a new level  $a^*$  for the higher signal. In the case where  $q^* > q_{\text{crit}}$ , so that  
 313  $a^* = \min(A_1) > a_1$ , such a system could be destabilized by the introduction of a signaller  
 314 that included  $a_1 \in A_1$ , which would enable individuals with qualities  $q^* > q > q_{\text{crit}}$  to  
 315 signal honestly to the benefit of themselves and the receiver. There will also be a  
 316 value  $q_{\text{min}}$  so that if  $q^* \leq q_{\text{min}}$ , (i.e. if  $q^*$  is sufficiently small), then (due to inequality 6)  
 317 the expected reward to the receiver will be at least as high if it changes to make choice  
 318 0 against all signals, and so again the system is not stable. This leaves a family of  
 319 possible “semi-honest” signalling systems with cutoff  $q^*$  such that  $q_{\text{min}} < q^* \leq q_{\text{crit}}$  that  
 320 might be stable in some circumstances (when the “honest” solution also exists). Note  
 321 that such alternative solutions are “semi-honest” in the sense that every individual  
 322 giving the higher signal is of better quality than every individual giving the lower  
 323 signal. However, some individuals with qualities near to (and on one side of) the  
 324 critical value will gain advantage by using the “wrong” signal from the receiver’s  
 325 viewpoint. Thus it is important to note that we do not claim that the fully honest signal  
 326 is the one that the population will evolve to. We have shown, however, that such a  
 327 system is a possible solution, and that all of the other potential solutions have the  
 328 same all-or-nothing property.

329

330 The general solution for our model is that signallers below a defined quality threshold  
 331 all signal using the lowest-cost signal that is possible, and receivers respond to this  
 332 signal with the choice that least benefits signallers; signals with quality above this  
 333 threshold all signal using the same signal, this is a higher cost signal than that used by  
 334 low-quality individuals and is the signal that leads to the same payoff to individuals of

the critical quality regardless of what the receivers do. Receivers respond to the higher-cost signal by adopting the behaviour (from a choice of two) that is more beneficial to signallers.

Thus, although signallers vary continuously in quality, they do not show continuous variation in signal strength at this equilibrium. Rather, the discrete nature of the behavioural responses to signals available to the receiver causes the receiver to be interested in categorizing signallers rather than fully evaluating their quality, and this in turn leads to signalling being restricted to a number of discrete levels, less than or equal in number to the number of behavioural options open to the receiver.

### **An example**

Let us consider a simple example where males of quality  $q$  signal to females, who can choose either to mate with a specific male or not.

For the female, there is no reward (or cost) for declining to mate  $V(q,0) = 0$ . Mating requires a fixed cost ( $\alpha$ ) and benefits increase linearly with the quality of the male. Thus, at its simplest  $V(q,1) = q - \alpha$ .

For the male, there is a cost for an individual of quality  $q$  to produce a signal of strength  $a$  given by  $a/q$ . There is an additional payoff of unity if the female chooses to mate and zero otherwise. Thus,

$$U(0,q) = -\frac{a}{q}, \quad U(1,q) = 1 - \frac{a}{q}.$$



359

360 Substituting these into (7) and (11) yields the solution  $a_1 = q_{\text{crit}} = \alpha$ .

361

362 Thus under fully honest signalling we predict that males with quality lower than  $q = \alpha$   
363 will signal using the lowest-cost signal available and will always be rejected by  
364 females; whereas males with a higher quality than this will signal at level  $\alpha$  and will  
365 always be mated with by females.

366

367 It is easy to see the rationality of this in the very simple case considered. At the  
368 equilibrium females always mate with males that offer a net benefit to them, and  
369 never mate with males that offer a net loss to them. Given this behaviour by receivers,  
370 the minimal-cost signalling of low quality males also seems easy to understand. Since  
371 these individuals are destined to be rejected by females, their signal can bring them no  
372 rewards and so the best strategy is to minimize the costs of signalling. However,  
373 investment in more expensive signalling is rational for the high quality individuals  
374 since they can convert this advertising into rewards (mating opportunities). Still they  
375 should be selected to invest just enough in advertising to both produce the desired  
376 behaviour in the receiver, and to prevent the best of the poor males from cheating. The  
377 payoff to low-quality, minimum-cost signallers is zero, the signal level adopted by the  
378 high-quality individuals is the cheapest signal that yields a net positive payoff to all  
379 individuals that use this signal (except any right on the threshold, who also receive  
380 zero).

381

382 **Discussion**

In this paper we have considered a model of signalling behaviour where the receivers have only a discrete number of possible responses to the signal. Our model predicts that even if signallers vary continuously in quality, and signals are received with perfect fidelity, these signals need not show continuous variation in signal strength. Rather, the discrete nature of the behavioural responses to signals available to the receiver causes the receiver to be interested in categorizing signallers rather than fully evaluating their quality, and this in turn leads to signalling being restricted to a number of discrete levels (at most equal in number to the number of behavioural options open to the receiver). Thus we predict that such signals will be commonplace when the behavioural responses of receivers are constrained to take a discrete number of values. Examples of this could include signalling of prey toxicity to predators, where predators can respond either by eating an individual signaller or rejecting the opportunity to eat it. Another example may be mate choice where the choice is again binary: mating with or rejecting the signaller. We thus expect such situations and such all-or-nothing signalling to be commonplace. However, there are other cases where the responses of signal receivers may be more continuously distributed. For example, in response to signal quality of a long-term social partner, a female bird may vary the investment that she makes in the eggs that will become their joint-offspring (Clutton-Brock 1991; Blount et al. 2000). This investment (say in levels of anti-oxidants committed to the eggs) is best seen as a continuously varying response, and so we would predict that the signalling behaviour of the males would not be well represented by the model considered here and (in the absence of perceptual errors) we would consider a continuously distributed signal by the males to be more likely.

Bergstrom & Lachman (1998) present a model that they use to suggest that honest signaling between relatives can be maintained in the absence of substantial

costs to signal production. The type of equilibrium that they consider are of the all-or-nothing type discussed here, where signallers of a range of qualities are grouped into a finite number of what the authors term “pools” with all individuals in the same pool producing the same signal. However, a very important difference between our approach and theirs is that a finite number of signal levels is a prediction of our model, whereas the signal being constrained such that only a finite number of signal types are possible is a fundamental assumption of their model. Our methodology does not involve any such constraint on signal production.

The all-or-nothing signalling predicted here may not be seen in situations where there is strong between-individual variation in the receivers in the value of the signallers to them. Consider the example of predators and chemically defended prey. Previously we have considered a critical value of toxins above which the prey becomes unattractive to the predators. There may be some circumstances where individual predators essentially agree on this critical value, in which case we would expect our model to hold. However, there may be other circumstances where there is considerable variation in this value between individual predators. This could be driven by variation between individuals in the need for the nutritional benefits of the prey (with hungrier individuals being prepared to accept higher toxin loads to avoid the risk of starvation) or variation in their ability to cope with the toxins (perhaps through variation in their current toxin burden): see Endler & Mappes (2004) for examples. If this variation in threshold of defence is large then this may cause the all-or-nothing type of signal predicted here to break down and be replaced by a more continuously-varying signal, as in [10].

Johnstone (1994) cited a number of influential papers that predict (in contrast to our model) that signal intensity should vary continuously in relation to the quality or need of the signaller: (Grafen 1990, Godfray 1991, Johnstone & Grafen 1992, Pagel 1993). In each case, it is possible to explain why these models make different predictions to ours. As already discussed, in Johnstone & Grafen (1992) wide receiver variation causes different receivers to wish to respond to many different signallers in different ways, making variation in signalling level viable. In Grafen (1990) and Pagel (1993) this difference is due to the cost function, which they make an explicit function of the error in perception of underlying signaller quality, so that there is a cost which continuously increases as a function to the size of the perceptual error. This is the situation we discussed in the introduction where all errors are considered to be costly. The exact mechanism underlying these costs is not defined in these papers, and choices available to the receivers (on receipt of a particular signal value) are not explicitly given. In Godfray (1991) the choices are explicitly given; these are the possible levels of provisioning by a parent to its offspring. This provisioning effort is considered to vary continuously, so there is a continuum of choices (rather than the binary choice considered here), and thus the scenario is different to ours, and (in the absence of perceptual errors) a continuously varying signal intensity is certainly plausible here.

Notice that the receiver strategy as we have defined it only describes responses to the two types of signal that are expected in the equilibrium situation. There may be occasional aberrant individuals that produce signals that are different from either of the two signals that form the equilibrium. It is likely that the receivers will treat such a signal in a way similar to whichever of the two equilibrium signals it most resembles,

with the similarity of response getting stronger as the similarity between aberrant and nearest-equilibrium signals increases. Such generalization across similar signal types is commonly observed empirically (Bradbury & Vehrencamp 1998). However if signals just below the higher signalling level are always treated as the higher signal, the signalling system will be destabilized, so there must be at least some probability of such signals being treated as a low signal for any system to be stable (this would only need to be small for small discrepancies, since the benefit from using a lower-cost signal is greatly outweighed by the cost of being interpreted as a low signal). Overall, the optimal strategy for receivers to deal with aberrant signals will depend on the exact biological mechanism that leads to the production of aberrant signals, since the fine detail of this mechanism will influence the probability distribution of individual signaller qualities ( $q$  values) associated with a particular aberrant signal strength. However, we might not expect to see natural receivers closely following this theoretical optimum strategy, since aberrant signals will be rare and so selection pressure shaping responses to such signals will be less than selection on responses to more commonly encountered signals. Rather we might expect to find between-receiver variation in response to aberrant signals (Arak & Enquist 1993), but with all receivers generally showing the rational behaviour of generalization across similar signals such that they treat aberrant signals (in particular high signals) in a way that is like their treatment of the most similar of the signals that makes up the equilibrium set.

In this paper we have been particularly interested in how an honest signalling system could work in our chosen scenario, and this has been our main focus. However, we found that we could not discount the possibility of what we called a semi-honest

482 system, where higher signals mean a better quality individual than lower ones, but  
483 where the cut-off is not that of the totally honest signalling system. It may be that such  
484 systems can be destabilized through the introduction of signalling errors, as in  
485 Johnstone (1994), or alternatively through receiver variation, and this would certainly  
486 be worth further investigation.  
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